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Optimizing conservation benefits for threatened beach fauna following severe natural disturbances

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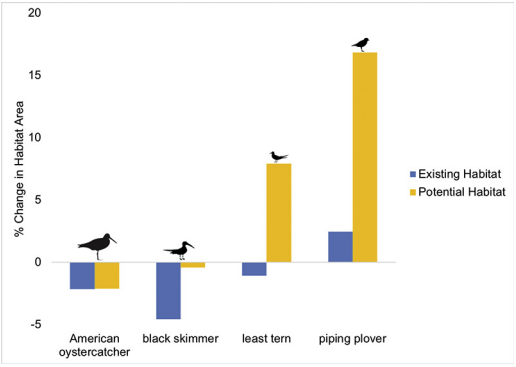
HIGHLIGHTS

- Wildlife habitat on beaches is reduced by human land use; land acquisition is rare.
- Coastal storms can benefit species by creating new habitat.
- Hurricane Sandy created nesting habitat for 3 of 4 avian species examined.
- Gains did not benefit birds because habitat was created outside the existing network of conservation areas.
- Flexible spatial conservation investments are a key input in storm-recovery planning.

GRAPHICAL ABSTRACT



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ABSTRACT

Wildlife on sandy beaches is often constrained by transformation of natural areas for human use, and opportunities for acquiring or restoring new habitat are rare. Storms can often force changes in land use naturally by reshaping coastal landforms, thereby creating high quality habitat; yet, wildlife requirements are seldom considered in post-storm recovery planning, and conservation practitioners lack suitable evidence to argue for the protection of habitats freshly formed by storms. Here we used a maximum-likelihood spatial modeling approach to quantify impacts of Hurricane Sandy (mid-Atlantic United States, October 2012) on nesting habitat of four bird species of conservation concern: American oystercatchers, black skimmers, least terns and piping plovers. We calculated the immediate storm-created changes (loss, persisting, gained) in nesting habitat under two levels of conservation protections: the current regulatory framework, and a scenario in which all potential habitats were under conservation protection. Hurricane Sandy resulted in apparent large gains for least terns (+181 ha) and piping plovers (+289 ha). However, actual gains were reduced to 16 ha for plovers and reversed for least terns (net loss of 6.4 ha) because newly formed habitat occurred outside existing reserve boundaries. Similarly, under the current management framework, black skimmer nesting habitat decreased by ~164 ha. We also tested whether birds benefited from newly created nesting habitat by identifying nest and colony locations for three years following Hurricane Sandy. All species overwhelmingly nested in habitat that existed prior the storm (76–98% of all nests/colonies); only a small percentage (≤17% for all species) occupied newly created

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habitat. We conclude that static spatial conservation efforts fail to capitalize on potentially large gains resulting from storms for several species and recommend flexible spatial conservation investments as a key input in post-storm recovery planning.

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1. Introduction

Sandy beaches and dunes on high-energy coastlines are highly dynamic landforms that are continually re-shaped by changes in sediment supply, wind, waves and tides (Davis and FitzGerald, 2009). Several species, including many of conservation significance, are reliant upon beaches or dunes throughout their lifecycle. Many have evolved a number of life history traits and behaviors in response to the physical attributes and dynamism of ocean beaches and dunes. For example, some exhibit physiological tolerance to environmental stresses (Gray, 1985), or modify their reproductive strategies to compensate for flood risk or sand burial (Maun, 1998; Thompson et al., 2001). Others change foraging behaviors to efficiently exploit pulses and spatial changes in food availability and shifts in habitat use as a response to significant habitat change (Erwin et al., 1981; Schlacher et al., 2014b).

Beaches are also important sites for human recreation, commerce and habitation, which can cause widespread and intensive human transformations of beach landscapes (Lockwood and Maslo, 2014). This development places significant and increasing pressures on the extent and quality of nesting and feeding habitats for beach-dependent species. In addition, birds attempting to breed, roost or feed in relatively undisturbed habitats are sometimes killed by human commensal predators (e.g., red foxes, cats, corvids; Ekanayake et al., 2015; Maslo et al., 2016b; Schlacher et al., 2015), or have restricted access to foraging resources (Greene, 2002; Heerhartz et al., 2014; Schlacher et al., 2016). Stark declines in populations of numerous coastal species of wildlife are regularly attributed to these threats. Alarmingly, maintaining remaining habitat patches of sufficient quality often fails to ensure a species' persistence (McClenachan et al., 2006).

Land use along existing coastlines is almost entirely designated, and changing existing regulation is difficult (Wescott, 2004). Continual human demand for coastal land to construct and renew housing and increase recreational opportunities results in limited opportunities for increasing habitat extent through land acquisition (McFadden, 2007; Tarlock, 2007). In addition, there is rarely any political will to increase conservation area extent because the ecological values and functions of dunes and beaches for wildlife are usually undervalued (Beatley, 2012; Jones et al., 2017). While significant natural events like storms can change the shape, size and configuration of coastal landscapes (Bergillos et al., 2017), land-use planning continues to operate on the premise that landscapes are static, thereby further limiting the flexibility of coastal habitat changes for conservation purposes.

Significant storms can lower dunes, scour vegetation and deposit large amounts of shell and wrack material (Masselink et al., 2016; Splinter et al., 2018). These processes reset the successional trajectory of the ecosystem and can create habitat features (i.e., overwash fans, ephemeral pools, and mottled substrates) known to be important for several beach-dependent species (Cohen et al., 2009; Rumbold et al., 2001; Wunderle et al., 2007). Extreme weather events can also cause significant damage to public infrastructure, housing and personal property (Hsiang et al., 2017). As a result, environmental regulations are often relaxed to facilitate human recovery efforts (e.g., waivers from U.S. Clean Air Act requirements after Hurrican Katrina, 2005; Gerrard, 2006; Ingram et al., 2006). Further, a common response to storm impacts is increased investments in coastal armoring (Rotimi et al., 2009). In most cases, no regulatory mechanisms or processes exist to identify whether and where suitable habitat has been created by storms for animals or how to legislate to maximize the potential conservation benefits of these changes. Despite widespread evidence that storms can actually enhance the size and quality of habitat for several threatened beach-dependent species on exposed shorelines (e.g., Cohen et al., 2010), arguments pertaining to wildlife conservation are rarely considered in storm recovery planning (Berke and Campanella, 2006; Mainka and McNeely, 2011). Therefore, empirical evidence generated through a consistent and systematic approach to identify newly created habitat worthy of future protection will make a more compelling case.

Here we used a maximum-likelihood spatial modeling approach to quantify the impacts of Hurricane Sandy, which made landfall on the mid-Atlantic United States in 2012, on existing nesting habitat of four beach-dependent bird species of conservation concern along the coast of New Jersey, USA. For each species, we calculated the net change in predicted nesting habitat across the study area and mapped where habitat was lost, persisted, or was created by the storm. Because availability of nesting sites is largely controlled by the intensity and type of recreational and maintenance activities (Maslo et al., in press), we compared the net change in habitat resulting from Hurricane Sandy under the current spatial configuration of conservation protection with a hypothetical scenario in which all of the coastline is protected. Using three years of post-storm nesting data, we examined whether target species capitalized on the newly created habitat areas. Through this work, we demonstrate the practicality and value of models to build evidence that conservation practitioners and land-use planners can use to secure protection of target species. Based on this new evidence, we provide guidance and recommendations on how to use flexible spatial conservation interventions following major storm impacts on sandy coastlines.

2. Materials and methods

2.1. Description of study area and existing conservation protections

This study was conducted within 5 km of the New Jersey, USA coastline (NJDEP, 2007), from Gateway National Recreational Area – Sandy Hook Unit, south to Cape May Point (~250 km; Fig. 1). We included all beaches, dunes, saltmarshes and tidal flats where the focal species could potentially nest. Fewer than half of the known birds nesting on New Jersey's beaches are in federally protected wildlife refuges (T. Pover, pers. comm; Heiser and Davis, 2017). Outside of protected areas, most beaches are used primarily for recreation, including sunbathing, action sports (surfing, kite-surfing, etc.), fishing, campfires, off-leash dogs, and off-road driving. In these locations, smaller nesting areas persist as part of negotiated beach management plans among site owners (i.e. municipalities, county parks), the United States Fish and Wildlife Service (USFWS) and New Jersey Endangered and Nongame Species Program (ENSP). Beach management plans are intended to provide long-term protection and recovery of protected species while balancing recreational use and storm protection. In areas under management for beach-nesting birds, pedestrian and vehicular access is restricted in nesting and foraging areas for all or part of the year (through closures and symbolic fencing), and there are restrictions on beach-raking, dogs, kite-flying, fireworks, and other active recreational activities.

2.2. Species habitat requirements

We studied four bird species of conservation concern in New Jersey: i) American oystercatcher (*Haemotopus palliatus*); ii) black skimmer

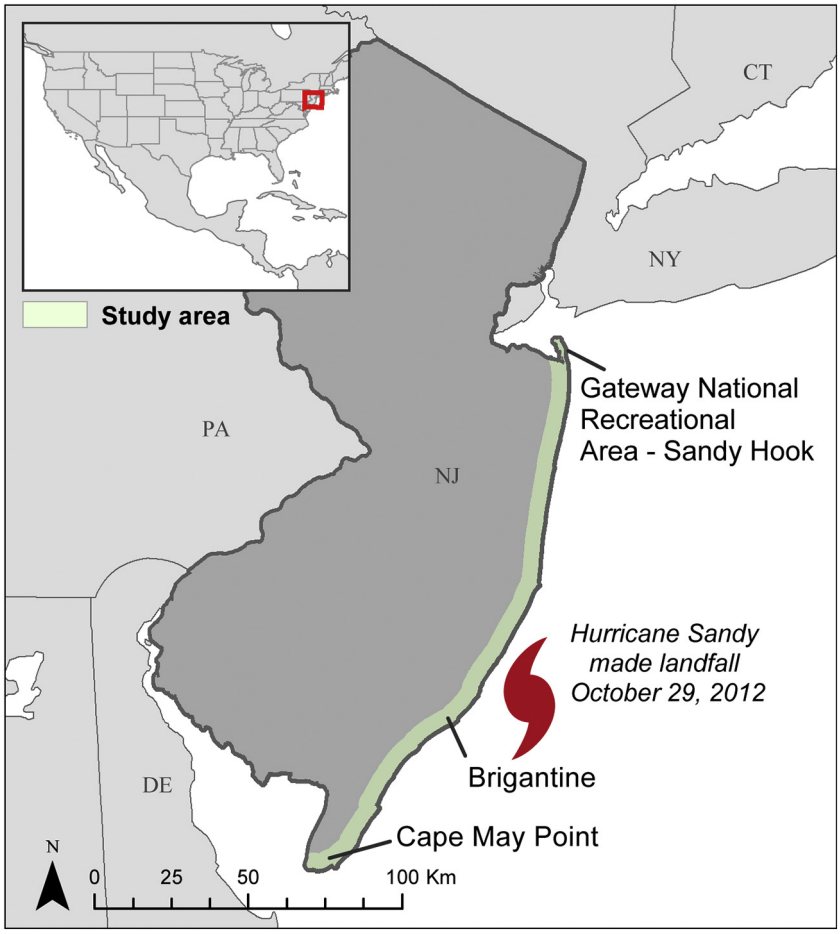

Fig. 1. The study area included all land and water within 5 km of the New Jersey (USA) coastline from Gateway National Recreation Area – Sandy Hook Unity to Cape May Point (~1040 km^2).

(*Rynchops niger*), iii) least tern (*Sterna antillarum*), and iv) piping plover (*Charadrius melodus*) (Table S.1). While these species broadly share nesting habitat on exposed dunes and beaches, a number of differences in life history traits create differences in species habitat requirements. American oystercatchers and piping plovers nest in solitary pairs (Cohen et al., 2010; McGowan et al., 2005). Black skimmers and least terns nest in colonies comprising up to several hundred pairs (Burger and Gochfeld, 1990; Erwin et al., 1981). Least terns and piping plovers are obligate beach-nesting birds; they occupy low-elevation areas with gently sloping, low-lying dunes, with their nests being typically located between the spring high tide mark and the seaward-facing toe of the foredunes (e.g., Cohen et al., 2009; Maslo et al., 2011). By contrast, American oystercatchers and black skimmers nest in a greater variety of habitat types, including open sandy beaches, dredge spoil islands, and saline marshes (Burger and Gochfeld, 1990; Maslo et al., 2016a; Rounds et al., 2004). American oystercatcher and piping plover chicks are precocial and feed on marine and terrestrial invertebrates along the intertidal zone and wrack line (Maslo et al., 2012; McGowan et al., 2005); black skimmers and least terns feed their young small fish obtained from the surf zone or other nearshore habitats (Foster et al., 2009; Paiva et al., 2008).

2.3. Hurricane Sandy

Hurricane Sandy made landfall near Brigantine, New Jersey (Fig. 1) on October 29, 2012 during a spring high tide. The area experienced maximum sustained winds of 130 km h^{-1}, a storm surge exceeding 2.5 m, continuous heavy rain (Buxton et al., 2013; Sopkin et al., 2014) resulting in widespread flooding over several days (Blake et al., 2013), and severe damage to coastal infrastructure and property (Comes and Van de Walle, 2014; Cutter et al., 2014). Changes to coastal landforms were significant but inconsistently distributed across the impacted area (Hauser et al., 2015; Roman, 2015; Sopkin et al., 2014; Zhai and Jiang, 2014). Some locations experienced severe beach erosion and reductions in dune height of up to 6 m, while other areas experienced significant accretion (up to 2 m) (Sopkin et al., 2014).

2.4. Modeling Hurricane Sandy's effects on nesting habitat

Existing published models (Maslo et al., 2016a; Maslo et al., in press) predicted the distribution of target beach-nesting birds species across New Jersey prior to Hurricane Sandy under both the current network of protected sites (hereafter, *existing habitat*), as well as under a hypothetical scenario in which all of coastal New Jersey is under conservation protection for beach-nesting birds (hereafter, *potential habitat*). Comparisons between these models show that human disturbance significantly reduces the quality of otherwise geomorphically suitable nesting habitat, rendering it unsuitable for breeding (Maslo et al., in press).

Species distribution models are a useful tool for optimizing the design and placement of conservation efforts (Moilanen et al., 2009; Rodríguez et al., 2007). They have been validated in a variety of contexts (Elith and Leathwick, 2009; Guisan et al., 2013; Guisan and Zimmermann, 2000), providing evidence to form the basis of adaptive management strategies (Guillera-Arroita et al., 2015; Kerr and Ostrovsky, 2003; Villero et al., 2017). To build species distribution models for each species, Maslo et al. (2016a) used a spatially explicit maximum entropy modeling software (Maxent version 3.3.3 k; Phillips et al., 2006), which is a widely

employed species distribution modeling platform that uses a deterministic, maximum-likelihood framework to analyze presence-only species occurrence data. Spatial areas are split into equal "cells," with the total area (or resolution) of each cell defined by the user. Maxent generates a probability of occurrence, or *suitability score* (from 0 to 1), for each cell, and then displays those scores visually as a map of predicted occurrence, with each cell (at a 10-m resolution; Maslo et al., 2016a) reflecting the species' probability of occurrence by color.

These models were trained on nest occurrence data for the pre-storm years 2007–2011 and tested on an independent dataset. Maslo et al. (2016a) tested eight predictor variables in the models (Table S.2), representing elevation and slope, land cover and distance to both the high tide line and to non-ocean foraging habitat. They characterized beach width (narrow vs wide shorelines), as well as adequate breeding territory size, by calculating the total area of sandy beach and marsh (separately) within 100 m of each cell. They also included differences among habitats with respect to level of human disturbance by classifying them into four levels of management interventions representing increasing protection status: 1) unprotected areas; 2) species precautionary areas; 3) species protection areas; and 4) closed areas. In unprotected areas, beaches are maintained for human use either during the summer (late May through early September) or throughout the entire year, and pedestrian access is permitted from the high tide line to the seaward toe of the primary dune. Recreational beach vehicles typically are permitted from October to April, while authorized vehicles servicing, for example, refuse pick-up and lifeguards are permitted all year. Precautionary areas have temporary no-rake and no-vehicle designations, but human access is only restricted if birds initiate nests. Species protection areas have more proactive interventions, including full breeding season beach-rake, vehicle, and dog prohibitions. In addition, anticipated nesting areas are delineated with symbolic fencing. Closed areas have no public access throughout the breeding season. All protected areas are monitored by state or federal wildlife agency personnel during the breeding season. With a few exceptions, signage, symbolic fencing, and agency presence effectively minimize human disturbance of breeding areas. Enforcement typically comes in the form of outreach and education (i.e. friendly conversations between monitors and trespassers). Egregious offenses (i.e. nest or egg destruction) are rare and handled by state conservation officers or the local police authorities. To calculate existing vs. potential habitat, Maslo et al. (in press) pooled the three original managed zones (closed, protection and precautionary areas) into a single 'protected' classification.

The models returned a probability of a nest occurrence for each target species for each 10-m cell across the study area. A cell was considered to be 'suitable' nesting habitat if its suitability score was greater than or equal to the calculated 10-percentile training presence threshold (i.e. the minimum suitability score above which 90% of the occurrence data fell; Maslo et al., 2016a). Suitability thresholds for each species were: 0.208 (American oystercatcher); 0.300 (black skimmer); 0.382 (least tern); and 0.474 (piping plover). For all species, land cover and distance to the high tide line were important predictors of nesting habitat. Distance to non-ocean tidal waters was important in determining American oystercatcher and black skimmer habitat, while beach size and width had more influence on least tern and piping plover nesting habitat. Elevation and slope had relatively little predictive power. Management zone was ranked among the top four predictors of nesting suitability for all species, and the total extent of suitable nesting habitat increased with the expansion of protection from human disturbance (i.e. total habitat area was always greater when protection from human disturbance was included).

In the current study, we focused on nesting habitat extent and quality following Hurricane Sandy. We first prepared a new set of environmental layers representing the geomorphology of the coastal landscape after Hurricane Sandy (Table S.2). We manually modified the pre-Sandy land use classification GIS shapefile (NJDEP, 2010) by overlaying it onto post-Sandy aerial imagery (NOAA, 2012) and re-drawing the polygons to accurately reflect the new land distribution. Once the land-use layer was consistent with the aerial imagery obtained after the storm, we recalculated the distance to non-ocean tidal waters, total beach area within a 100-m radius, and total marsh area within a 100-m radius (Table S.1; Maslo et al., 2016a). We replaced the pre-Sandy elevation GIS layer with one generated from post-Sandy light ranging and detection (LiDAR) data (flown during the week immediately following the storm; USGS, 2016), from which we also re-calculated slope. Finally, we measured the Euclidean distance to the high tide line based upon the wet-dry interface documented from the post-Sandy orthoimagery and a post-Sandy shoreline GIS layer (NOAA, 2014; Schupp et al., 2005). We projected our model onto the post-storm GIS landscape, applying the 10-percentile training presence of the model outputs (as before) as a threshold to determine whether a given cell in the study area was suitable for nesting by each target species (Table S.3).

To calculate the area of habitat for each species that was lost after the storm, persisted throughout the storm, or was newly created by the storm, we overlaid model outputs after the storm with matched outputs created before it. We defined 'lost' habitat as cells with probabilities of occurrence falling below the suitability threshold after the storm. We considered a cell as having persisting habitat if its probability of occurrence remained above the suitability threshold after the storm. We categorized newly created habitat as cells with probabilities of occurrence that increased above the suitability threshold after Hurricane Sandy. Finally, we calculated the net change in *potential* habitat and the *existing* habitat extent for each species associated with the storm.

2.5. Evaluating avian response to storm-induced habitat changes

Regardless of the impacts of Hurricane Sandy on the total potential habitat area theoretically possible under full protection, beach maintenance and recreational activities within the study area reduce nesting availability primarily to areas currently under conservation protection (Maslo et al., in press). This raises the question of whether severe coastal storms truly increase the habitat available to beach-nesting birds when anthropogenic constraints are considered. Consequently, to test whether birds actually benefitted from newly created nesting habitat, we plotted observed American oystercatcher and piping plover nest locations as well as black skimmer and least tern colony locations for three years following Hurricane Sandy (2013–2015) onto the post Sandy existing habitat model output for each species. For American oystercatchers and piping plovers, we counted the number of nests occurring each year in lost, persisting or newly created habitat. Because black skimmers and least terns are colonial nesters, the NJ Endangered and Nongame Species Program does not record locations of specific nests. Therefore, for these species we calculated the total area occupied by a colony that occurred in each habitat category each year.

3. Results

3.1. Quantifying beach-nesting bird habitat changes resulting from Hurricane Sandy

Hurricane Sandy modified the extent and distribution of coastal habitat types within the study area. Storm surge and wave action blew out nearly 4% of the vegetated dunes and increased the extent of bare beach substrate by ~6.5% (Table S.3). Mud flats and low saline marsh habitats were eroded, increasing the total coverage of tidal bays and tidal ponds by ~0.5% and 10%, respectively. In many locations, Hurricane Sandy reset the successional trajectory of the coastline, creating low-lying, sparely vegetated substrates important for beach-nesting bird breeding (Burger and Gochfeld, 1990; Gochfeld, 1978; Maslo et al., 2011; McGowan et al., 2005).

The storm changed the area of suitable nesting habitat for all species, but directions and patterns of change were dependent on the individual species' requirements. Potential habitat extent decreased slightly for

Table 1
Changes to bird nesting habitat resulting from Hurricane Sandy. Potential habitat represents the total predicted habitat area in the absence of human disturbance (or complete protection from it via intense management interventions along all of the coastline). Existing habitat considers human disturbance as a factor influencing habitat suitability.

	Pre-storm habitat area (ha)	Post-storm habitat area (ha)				Net change in habitat area (ha)
		Lost	Persisted	Created	Total	
American oystercatchers						
Potential habitat	5079.6	−638.5	4449.1	522.8	4963.0	−107.7
Existing habitat	4920.1	−628.2	4291.5	523.5	4815.0	−105.1
Black skimmers						
Potential habitat	4381.5	−688.6	3714.6	648.5	4361.8	−19.7
Existing habitat	3605.3	−657.6	2947.4	493.7	3441.2	−164.1
Least terns						
Potential habitat	2265.6	−285.1	1979.5	466.7	2446.2	180.6
Existing habitat	591.7	−155.4	436.1	149.2	585.3	−6.4
Piping plovers						
Potential habitat	1726.6	−288.5	1436.9	578.5	2015.4	288.8
Existing habitat	649.1	−173.0	475.9	189.1	665.0	15.9

American oystercatchers (107.7 ha) and black skimmers (19.7 ha l; Table 1), these losses occurred mainly in saline marsh areas that became inundated or eroded (Figs. 2, 3). By contrast, potential habitat expanded for least terns (180.6 ha gain or 7.9%) and piping plovers (288.8 ha gain or 16.7%; Table 1); these gains were largely driven by dune destruction and the scouring of beach vegetation to create wide flat sandy areas (Figs. 4, 5).

For American oystercatchers changes in nesting habitat associated with the storm were similar whether the extent of conservation was considered or not (i.e. human disturbance did not influence storm effects on nesting habitat; Fig. 2). By contrast, storm impacts on nesting habitat for the other species depended on the extent of conservation. Black skimmers lost 20 ha of nesting habitat in the fully protected scenario; this loss increased to 164 ha under the current management regime (Table 1). This net change was largely driven by suitable nesting habitat 'added' in areas outside existing reserves. Similarly, storm-induced habitat gains for piping plovers and least terns largely occurred in areas not currently protected under existing beach management plans (Fig. 7). For piping plovers, there was only a modest positive storm effect of a 16 ha net gain overall under the current management

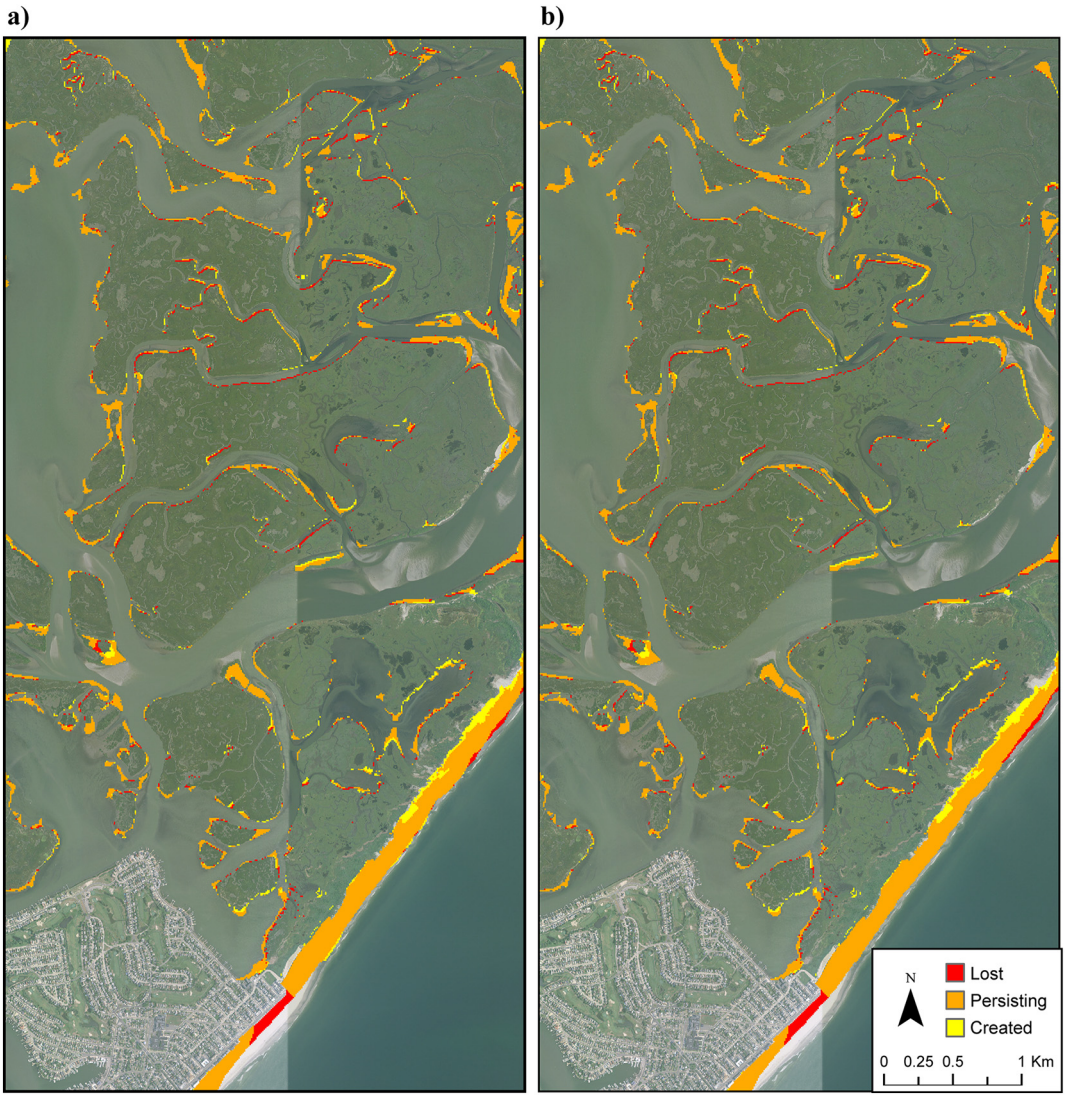

Fig. 2. Example of the effect of Hurricane Sandy on American oystercatcher nesting habitat. The maps illustrate very little difference in a) potential and b) existing habitat that was lost, persisting, or newly created after Hurricane Sandy (October 2012) in Brigantine, New Jersey, USA.

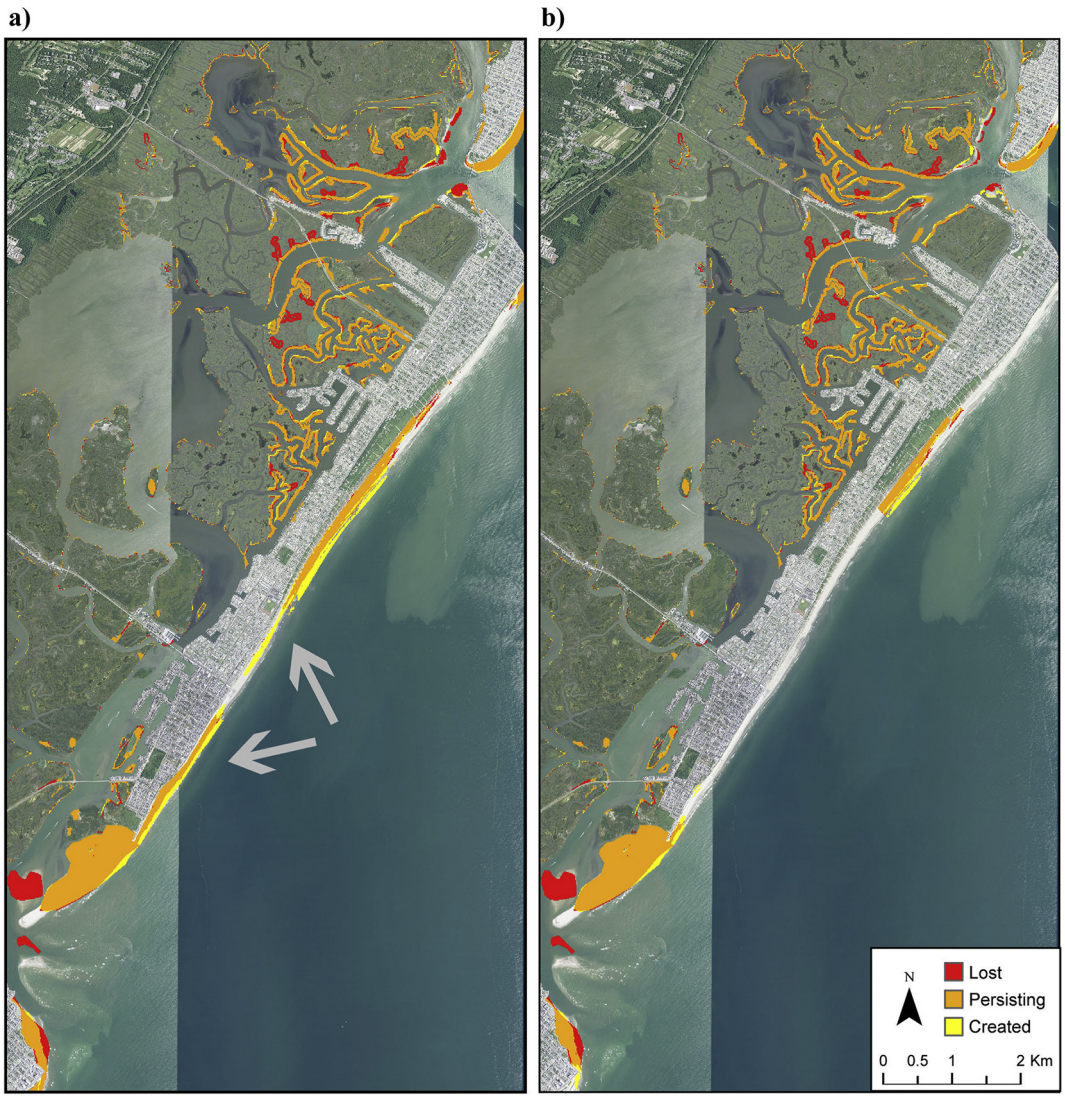

Fig. 3. Example of the effect of Hurricane Sandy on black skimmer nesting habitat. Arrows highlight the difference in a) potential and b) actual that was created after Hurricane Sandy (October 2012) in Stone Harbor, New Jersey, USA.

regime, whereas full protection is predicted to result in an 18-fold increase of new habitat to 290 ha (Table 1; Fig. 6). For least terns, Hurricane Sandy caused an asymmetrical effect on nesting habitat area depending on the level of protection from human disturbance: under the current management regime a small (−6 ha) net loss of habitat was caused by the storm, whereas a considerable expansion of nesting habitat is predicted under the full protection scenario (Table 1). As was the case for piping plovers, there was a proportionally smaller area of nesting habitat that resisted storm changes under the current regime (current 74% vs 87% full protection) and proportionally more area was lost (current −26% vs −13% full protection; Table 1).

3.2. Avian response to habitat changes

Although some new nesting habitat areas were created by Hurricane Sandy, all species overwhelmingly nested in habitat that existed prior the storm (persisting habitat; Table 2). From 2013 to 2015, 89% of American oystercatcher and 68% of piping plover nests occurred in habitat that persisted throughout the storm (Table 2). Similarly, 81% of the total area occupied by nesting black simmer colonies and 69% of least tern colonies over the same timeframe were initiated in persisting habitat areas. By contrast, only 2% of all American oystercatcher nests and ≤5% of the total black skimmer and least tern colony area occurred in newly created habitat areas; piping plovers used newly created habitat areas somewhat more, with 14% of all nests occurring in new habitat between 2013 and 2015. With the exception of black skimmers, all species increased the use of newly created habitat areas over time (Table 2); this pattern was particularly notable for least terns where use of newly created nesting areas increased ~5-fold over three years following the storm.

4. Discussion

4.1. Effects of storms on avian nesting habitat on sandy beaches

Severe coastal storms can reset the successional trajectory of sandy beach and dune ecosystems by scouring vegetation, redistributing sand and other materials, and modifying topography (e.g., Backstrom et al., 2008; Haerens et al., 2012). These physical processes can be beneficial to beach-dependent species that rely on natural coastal dynamics to maintain suitable habitat. Storms create habitat features (e.g., overwash fans, ephemeral pools, etc.) that can improve survival and reproductive success for many species (Davis et al., 2001; Erwin, 1996; Maslo et al., 2011), thus they potentially play an important role in maintaining population viability. We show here that least terns and piping plovers in New Jersey experienced net nesting habitat gains of ~8% and 16%, respectively,

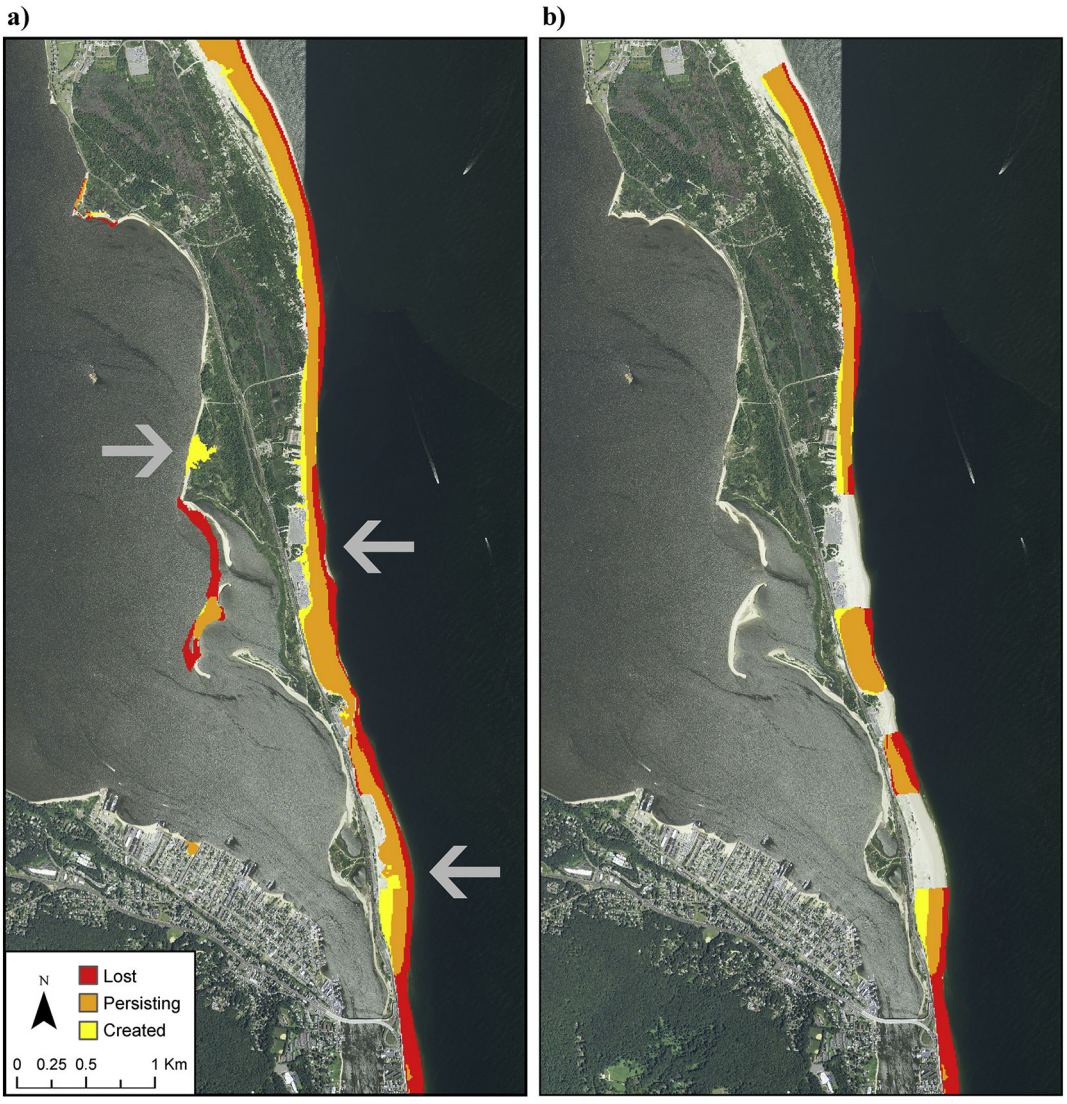

Fig. 4. Example of the effect of Hurricane Sandy (October 2012) on least tern nesting habitat in Gateway National Recreation Area – Sandy Hook Unit, New Jersey, USA. Arrows depict areas of a) potential habitat created in areas that, if under conservation protection, would have offset losses elsewhere. Under the b) existing network of protected areas, these areas are unsuitable for nesting.

as a result of Hurricane Sandy under current protection regimes. Habitat additions were largely due to the creation of wide, open sandy areas through the destruction of dunes and scouring a vegetation (Fig. S.3). For beach-nesting birds, ideal locations for nesting occur far from both the high tide line and the seaward toe of the foredune (Maslo et al., 2011; Mazzocchi and Forys, 2005). Such locations offer nests both protection from storm tides, as well as lowered detection probability by avian and mammalian predators (e.g., Lima, 2009, Van De Pol et al., 2010). Dune blowouts also create access to backbay foraging locations on barrier beaches, which is important for promoting fledging success of newly hatched plover chicks (Loegering and Fraser, 1995). These generalities notwithstanding, storm impacts on coastal geomorphology are highly dependent on multiple physical factors that vary widely among storms. Tidal stage, wind speed and direction, location of storm landfall, among other factors, dictate the extent and spatial positioning of associated shoreline modifications (e.g., erosion and accretion areas, dune breaches, etc.). Severe storms can reduce habitat through erosion of beaches, marshes and tidal flats or lowering of previously suitable elevations to levels where flood risk becomes acute. Where total pre-storm habitat is expansive (in the case of species with flexible habitat requirements), storm impacts may not be severe in the short term. Black skimmers and American oystercatchers in our study area lost only 0.4% and 2%, respectively, of their total habitat extent due to Hurricane Sandy.

In the absence of human settlement, local habitat losses may generally be offset by gains in other areas. However, we show here that existing static coastal regulations and human-driven storm recovery efforts can negate these positive impacts if newly created habitat is not identified and protected. Under a scenario where all of the coastline is protected to benefit breeding birds, despite losing ~289 ha of existing nesting area, piping plovers experienced a net gain of ~289 ha (16% increase) because the storm created twice the amount (+579 ha) of habitat that was lost (Table 1). However, much of this newly-created habitat was located in areas that are currently not actively managed for birds (Figs. 5, 7), and the actual (factoring in human disturbance) habitat gains for this species was a much more modest 16 ha (2%). Thus, lack of spatially comprehensive habitat management fails to capitalize on potentially very large gains in habitat that can be created by storm-driven changes to the topography of exposed beaches and coastlines. For black skimmers, losses under the current conservation protection framework were 12 times greater than if protections were allowed to shift in response to physical habitat changes (Table 1). In the extreme case, the overall impact of Hurricane Sandy on least terns shifted from an appreciable net gain in habitat (8%) to a net loss (Fig. 4). Given that

Fig. 5. Example of the effect of Hurricane Sandy (October 2012) on piping plover nesting habitat in Island Beach State Park and Barnegat Light, New Jersey, USA. The figure illustrates an appreciably larger extent of newly created a) potential habitat than what b) exists under the current network of protected sites.

various technologies exist to rapidly monitor landform changes after a storm, our results underscore the conservation importance of creating flexible reserve boundaries to mitigate losses in other locations.

Because human disturbance (or protection from it) significantly influences habitat suitability, birds will not likely use newly-created habitat that is not protected from detrimental human activity. Therefore, the conservation benefits of resetting the successional trajectory of coastal habitat are largely diminished if spatial conservation is not responsive and dynamic. In the three years following Hurricane Sandy, ≥68% of all nests and colony areas were established in habitat that persisted after the storm (Table 2). The majority of persisting habitat occurred in, and likely because of, existing conservation protected areas (Fig. 5). This pattern was especially strong for American oystercatchers and black skimmers, where 89% of nests and 81% of the total colony area, respectively, occurred in persisting habitat. Beach-nesting birds typically exhibit high site-fidelity (Erwin et al., 1981), so continued use of previous nesting sites is expected. However, birds that return to sites where habitat was lost must select new breeding territories and would likely select unoccupied habitat to reduce competition (Forstmeier, 2002). In addition, post-breeding individuals and juveniles investigate new nesting sites after the breeding season in late summer/early fall (Davis et al., 2017; Faaborg et al., 2010). Newly created habitat protected from human disturbance would likely be attractive to prospecting birds (Maslo et al., in press), thus increasing the number of nests initiated over time within the region. In our study, use of newly created habitat increased over time for three of the four species studied. In particular, piping plovers increased their use of new habitat by 4%, with 16% of the total statewide nests occurring in newly created habitat by 2015 (Table 2). This pattern appears driven by a shift in nesting at the Holgate Unit of the Edwin B. Forsythe National Wildlife Refuge, a ~115-ha undeveloped portion of a barrier island that is closed to the public during beach-nesting bird season. Prior to the storm, nesting habitat primarily existed at the southern tip of the site. Hurricane Sandy produced several overwash fans across the northern portion of the site. In the breeding season immediately following the storm, the majority of piping plover nests occurred within the previous nesting footprint at the southern tip. The next two years demonstrated a marked shift of nesting attempts to the newly-created overwash fans.

While few in numbers, nests also increased over time in areas not predicted to be suitable by the models. We predicted nesting habitat distribution across the study area based upon environmental data characterizing the immediate post-Sandy landscape; beach-nesting birds initiated breeding 5–6 months after the storm. In particular, our elevation data was generated from National Oceanic and Atmospheric Administration (NOAA) light ranging and detection (LiDAR) flights within a week after the storm made landfall. Flood waters may not

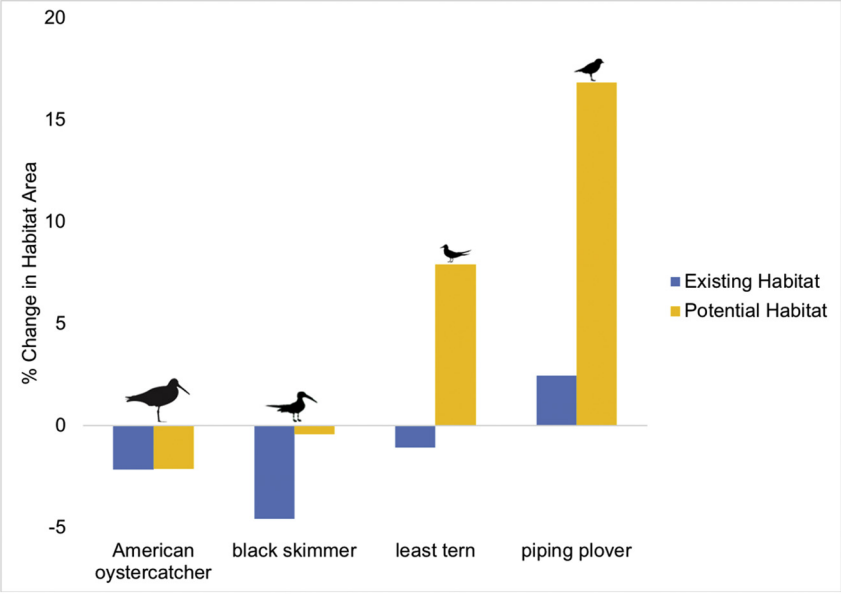

Fig. 6. Net percent change in extent of suitable nesting habitat for target species in New Jersey, USA resulting from Hurricane Sandy (made landfall October 29, 2012). Potential habitat considers only environmental predictors of nesting habitat suitability, while actual habitat incorporates the level of human disturbance protections and area has when quantifying its suitability for nesting.

have receded fully in some areas; thus, our models may have slightly underpredicted total suitable habitat extent across the study area. Regardless, we demonstrate that physical changes to the landform and vegetation cover that can benefit nesting birds will not translate into increased nesting success if protection from human disturbance does not follow suit. It is therefore critical that newly created habitat be identified and protected during the storm recovery process.

4.2. Management recommendations/considerations

Natural disasters cause significant damage to people, personal property, and infrastructure. They also cause severe impacts on natural resources and the species they support. However, wildlife agency representatives are rarely included in decision making processes during the post-storm recovery (Fox-Lent et al., 2015). Because on-the-ground storm response activities also often commence quickly after a storm, having wildlife officials involved at this early juncture is critical in identifying newly created habitat and involve wildlife experts in the response effort. Representation for wildlife considerations must continue throughout the recovery period.

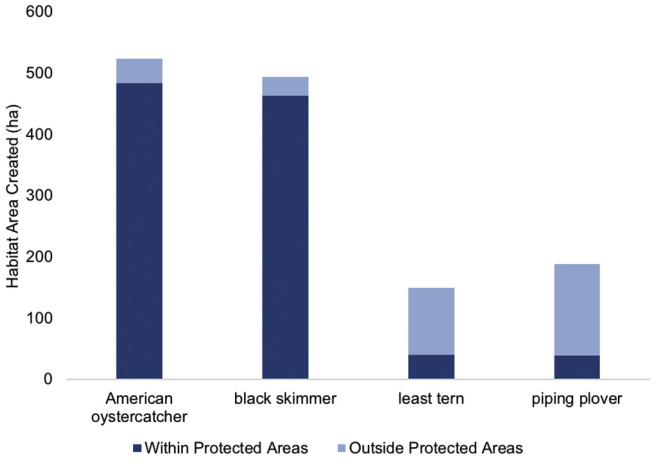

Fig. 7. Proportion of modeled total habitat created within and outside protected areas for target beach-nesting bird species in New Jersey, USA after Hurricane Sandy (October 2012).

Protective measures to reduce human disturbance during the nesting season increase the suitability of a site and can promote reproductive success. Beach raking, sand scraping, and off-road vehicles degrade beach and dune habitat (Defeo et al., 2009; Schlacher et al., 2014a). Curtailing these activities in and around identified habitat areas throughout the year can slow the rate of succession through natural coastal processes, thereby maintaining the habitat for a longer time period. Habitat suitability may increase due to the formation of microhabitat features important in nest-site selection (i.e. incipient dunes,

Table 2
Nest and nesting colony locations for beach-nesting birds in New Jersey, USA in response to habitat changes resulting from Hurricane Sandy, 2013–2015.

	# of nests occurring in habitat that:		
	Was lost	Persisted	Was created
American oystercatchers			
2013	2 (1%)	174 (98%)	1 (1%)
2014	1 (1%)	179 (96%)	5 (3%)
2015	7 (4%)	184 (91%)	9 (5%)
All years	10 (2%)	537 (95%)	15 (3%)
Piping plovers			
2013	5 (4%)	98 (83%)	16 (13%)
2014	7 (7%)	76 (76%)	17 (17%)
2015	3 (2%)	96 (79%)	23 (19%)
All years	15 (4%)	270 (80%)	56 (16%)
	Total area in hectares of nesting colonies occurring in habitat that:		
	Was lost	Persisted	Was created
Black skimmers			
2013	0.94 (6%)	14.3 (93%)	0.12 (<1%)
2014	0.34 (4%)	7.1 (94%)	0.12 (2%)
2015	0.09 (2%)	4.6 (97%)	0.05 (1%)
All years	1.37 (5%)	26.0 (94%)	0.29 (1%)
Least terns			
2013	2.10 (4%)	46.5 (94%)	1.08 (2%)
2014	8.41 (10%)	65.6 (86%)	2.97 (4%)
2015	2.10 (4%)	27.8 (81%)	5.19 (15%)
All years	12.6 (8%)	139.9 (86%)	9.24 (6%)

shell substrate, sparse vegetation growth). For newly created areas it may be beneficial to protect them from human interference especially during late summer and early fall, when prospective breeding pairs inspect potentially new breeding sites (Davis et al., 2017).

Management units with identified potential nesting habitat should be required to maintain a minimum protected area for beach-nesting birds, established through negotiations between management units and regulatory agencies. If the wildlife agency determines that reproductive success of birds nesting in identified habitat within a management unit is compromised due to high recreational use, mitigation for lost habitat should be sought. Prior to the nesting season, wildlife management agencies should modify the boundaries of the existing protected area, based on current habitat features.

It is important to note that implementation of management may not result in immediate occupancy by beach-nesting birds (Payo-Payo et al., 2017). Individuals have high site fidelity and typically return from migration to the sites in which they have previously nested (Cohen et al., 2006). Furthermore, as the condition of other habitats degrade, availability and ongoing maintenance of new suitable habitat may be important to maintain local/regional populations. Some level of protection should be maintained regardless of species' presence to maintain available habitat and encourage colonization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.08.319.

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